

**Life History of *Trupanea imperfecta* (Coquillett) on *Bebbia juncea* (Bentham) Greene in the Colorado Desert of Southern California (Diptera: Tephritidae)**

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*Abstract.*—*Trupanea imperfecta* is monophagous on the desert shrub, *Bebbia juncea* (Asteraceae), in southern California. Each female deposits one to three eggs singly or in a small cluster in a young capitulum. The larvae feed on the floral tubes and achenes and sometimes score the receptacle of the immature florets. The larvae pupariate towards the center of the heads individually or in clusters. Adults emerge from mature heads shedding achenes. This tephritid may be either univoltine or bivoltine; consequently, the adults may live as long as a year. Adults are thought to avoid the dry desert summers when their host plants are dormant by foraging as adults in reproductive diapause along streams and in meadows in the mountains. *Eurytoma* sp. and *E. vernonia* Bugbee (Eurytomidae), *Pteromalus purpureiventris* (Ashmead) (Pteromalidae), and *Torymus* sp. (Torymidae) are reported as primary, solitary, hymenopterous parasites of the larvae and pupae. *Horismenus* sp. (Hymenoptera: Eulophidae) is reported as a hyperparasite; whereas, *Mesopolobus* sp. (Hymenoptera: Pteromalidae) functions as a primary/hyperparasite.

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As presently known, *Trupanea* is the largest and most commonly encountered genus in the subfamily Tephritinae in California (Foote and Blanc 1963, Goeden unpubl. data). But knowledge of most species of *Trupanea* is scant and restricted mainly to their taxonomy (Foote 1960, Blanc and Foote 1987), distributions (Foote 1960, Foote and Blanc 1963), and host-plant affinities (Wasbauer 1957, Goeden 1985). The biologies of only a few species have been studied, i.e., *T. actinobola* (Stegmaier 1968), *T. bisetosa* (Coquillett) (Cavender and Goeden 1982), and *T. conjuncta* (Adams) (Goeden 1987). Herein, I describe the life history of *T. imperfecta* (Coquillett).

*Taxonomy.*—First described as *Urellia imperfecta* by Coquillett (1902), *T. imperfecta* additionally was described and illustrated in part by Malloch (1942) (as a *Trypanea*) and by Foote (1960) and Foote and Blanc (1963) (as a *Trupanea*).

*Distribution and hosts.*—Foote (1960) and Foote and Blanc (1963) recorded this tephritid from Arizona, California (mainly), and Nevada. However, like its principal host plant, *Bebbia juncea* (Bentham) Greene (Asteraceae), *T. imperfecta* may range into southern New Mexico, western Texas, and adjacent parts of northern Mexico (Benson and Darrow 1981).

During a faunistic survey of *B. juncea* from 1983 to 1986, *T. imperfecta* consistently was reared from mature capitula sampled throughout the range of this plant species in the Colorado Desert of southern California (Goeden and Ricker, unpublished

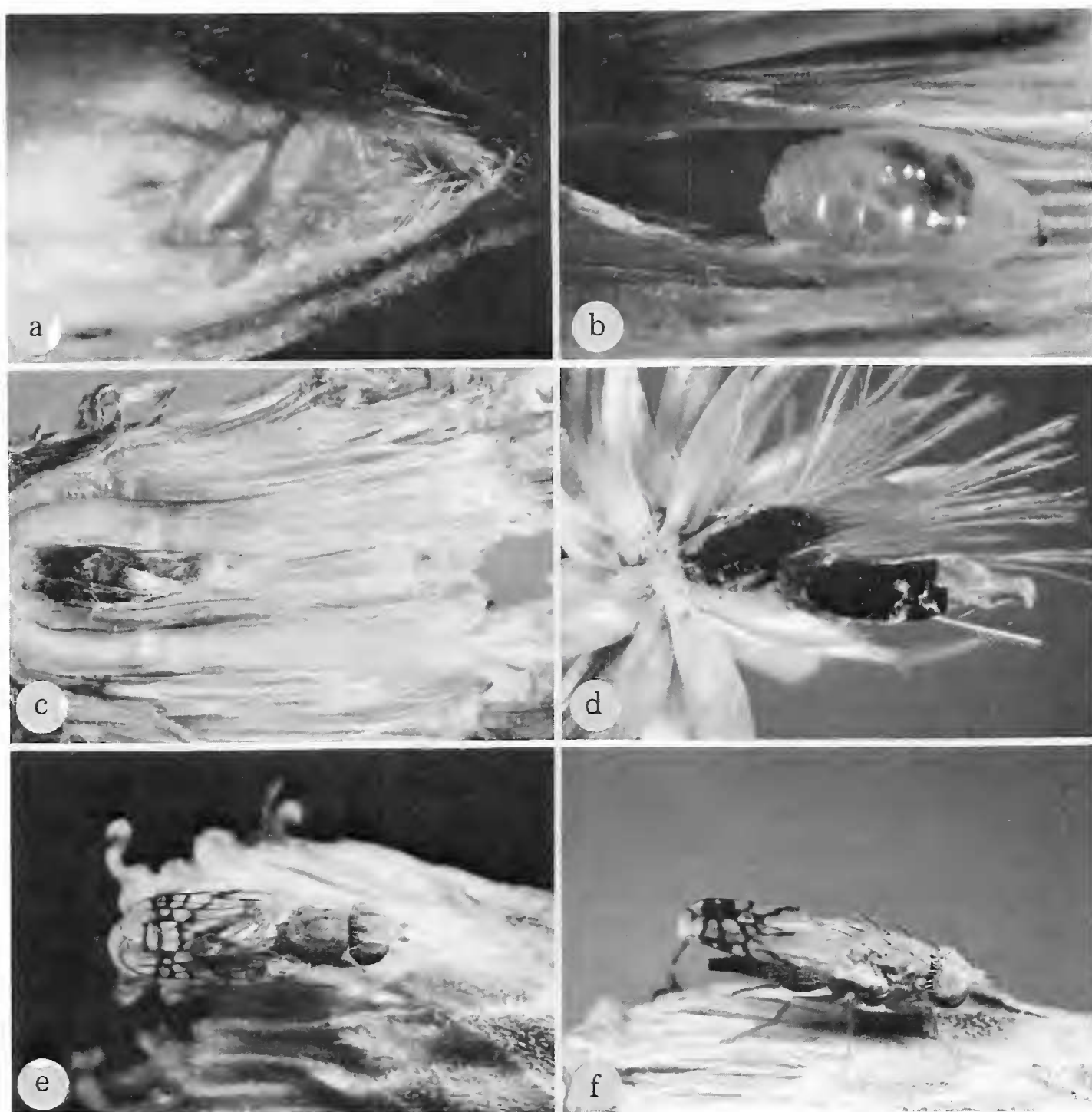


Fig. 1. Life stages of *Trupanea imperfecta*. (a) Two eggs in young capitulum, 22x. (b) Third instar, 13.5x. (c) Puparium in center of head of *Bebbia juncea*, 6x. (d) Two empty puparia attached to mature capitulum that has shed its achenes, 7x. (e) Adult male, 7x. (f) Adult female, 8x.

data and rearing records listed below). Moreover, no other tephritid was reared from these capitula, which supported the suggestion by Goeden (1985) that the record for *Trupanea pseudovicina* Hering from *B. juncea* in Wasbauer (1957) probably was erroneous, or atypical and rare.

Desert locations for *B. juncea* capitula sampled on the dates indicated, and from which *T. imperfecta* were reared, are listed chronologically and by county: Imperial Co.: Signal Mountain, 29 xi 1984; Wister, 29 xi 1984, 13 iii 1986; Painted Gorge, 12 xii 1984, 19 iii 1986; Sunrise Butte, 12 xii 1984, 30 i 1985, 20 iii 1986; Black Mountain, 7 i 1985; Indian Well, 12 iii 1986; Tumco, 13 iii 1986; Travertine Rock, 19 iii 1986; Imperial Highway, 19 iii 1986; Palm Canyon Wash, 20 iii 1986; Riverside Co.: West Bradshaw Trail, 12 i 1983, 23 iii 1983; Chino Canyon, 9 iii 1983, 13 iv 1983, 27 iv 1983, 13 v



1983, 25 v 1983, 7 vi 1983, 21 vi 1983, 7 vii 1983, 19 vii 1983, 5 viii 1983, 19 viii 1983, 19 ix 1983, 3 x 1983, 1 xi 1983, 15 xi 1983, 29 xi 1983, 13 xii 1983, 4 i 1984, 18 i 1984, 31 i 1984, 14 ii 1984, 29 ii 1984, 13 iii 1984, 29 iii 1984, 11 iv 1984, 24 iv 1984, 8 v 1984, 21 v 1984; Berdoo Canyon, 3 i 1985, 9 iii 1986; Salt Creek Wash, 28 xi 1984; Big Morongo Canyon, 9 ix 1986; Mission Creek, 9 ix 1986; Desert Center, 16 ix 1986; Painted Canyon, 16 ix 1986; San Diego Co.: Clark Dry Lake, 26 i 1983.

Goeden (1985) reported a single female of *T. imperfecta* reared from a mature capitulum of *Ambrosia ilicifolia* (Grey) Payne, although bulk samples of these heads commonly yielded only *Euaresta stigmatica* Coquillett or *Euarestoides acutangulus* (Thomson) (Goeden and Ricker 1976). Similarly, a single female of *T. imperfecta* was recorded by Goeden (1985) from *Coreopsis gigantea* (Kellogg) Hall, the capitula of which usually only contained *Dioxyna picciola* (Bigot) (Goeden and Blanc 1986). Thus, both records involved atypical hosts for *T. imperfecta*. "Mistaken" oviposition in heads of normally unattacked plant species growing closely to and stimulated by numerous capitula of a favored host species probably at least accounted for the atypical record for *A. ilicifolia*, i.e., representing what Goeden (1985) called a "spill-over effect."

Replicated rearings of bulk samples of mature capitula from 93 genera and 238 species of California Asteraceae since 1980 suggest that *T. imperfecta* essentially is monophagous on *B. juncea* (Goeden unpublished data). Foote and Blanc (1963) listed only one rearing record for *T. imperfecta* from *B. juncea* in California, but reported records for adults swept from species of *Chrysothamnus*, *Dicoria*, *Encelia*, *Eriogonum* (Polygonaceae), *Gnaphalium*, *Gutierrezia*, *Hyptis* (Lamiaceae), and *Lepidospartum*. Besides discounting the two non-Asteraceae as obvious non-hosts, the fact that none of the remaining genera have yet yielded a single reared specimen of *T. imperfecta* demonstrates the misleading nature of these sweep records as indicators of the larval food plants of this tephritid. This limitation of sweep records also was discussed by Goeden et al. (1987) relative to hosts of *Neotephritis finalis* (Loew) and to tephritids swept from *Hymenoclea salsola* Torrey and Gray by Goeden and Ricker (1986).

## BIOLOGY

The biology of *T. imperfecta* was studied largely in the field, or in the laboratory with field-collected material, during the faunistic survey of *B. juncea* noted above. Additional field observations were made in conjunction with my study of *T. conjuncta* (Goeden 1987) in Chino Canyon, 1 km NW of Palm Springs, Riverside Co., during 1983–1986.

*Egg*.—Newly laid eggs (Fig. 1a) are smooth, shiny, white and elongate-ellipsoidal, with a reduced, button-like, anterior pedicel, like those of *T. bisetosa* and *T. conjuncta* (Cavender and Goeden 1982, Goeden 1987). Fifty-one field-collected eggs averaged  $0.68 \pm 0.005$  ( $\pm$  SE) mm in length and  $0.19 \pm 0.001$  mm in greatest width. The pedicels averaged  $0.02 \pm 0.000$  mm in length. Thus, the eggs and pedicels are slightly shorter, but about as wide as those of *T. bisetosa* and *T. conjuncta*.

Most eggs were oviposited into immature heads of *B. juncea* that measured about 3 mm wide and 3 to 5 mm externally from base to apex, where the tips of the outer phyllaries converged. Eggs were laid loosely, and singly or in laterally touching groups of two to five (Fig. 1a). The orientation of their long axes ranged from perpendicular to parallel with the receptacle surfaces, and at various angles in between, but

mostly nearest the former plane, with their pedicels directed away from the receptacles (Fig. 1a). Some eggs were inserted between and parallel to the outer ranks of phyllaries, some alongside and parallel to the receptacle bracts, some pierced these bracts, and still others were oviposited within the open space above the layer of tiny buttonlike, unelongated floral tubes beneath the overlapping phyllaries.

Seventeen field-collected immature heads collected at Travertine Rock, Imperial Co., on 26 i 1983, contained an average of 5 (range, 2 to 9) eggs of *T. imperfecta*. Forty-six immature heads collected at Chino Canyon on 26 ii 1985 also contained an average of 5 (range, 1 to 14) eggs. These eggs were laid individually or in small clusters at slightly different angles (Fig. 1). In some cases, the eggs showed obvious differences in embryony between clusters in the same heads, indicating that they probably were oviposited by different females.

*Larva.*—Dissections of field-collected heads indicated that a newly hatched first instar usually entered a floral tube initially and fed on its contents. If the larva already was located centrally in the head and alone there, it continued to excavate this floret, and by the second or early third instar, entered the achene and completed its larval development there or in an adjacent achene (Fig. 1b). If the larva hatched on the periphery of a head, it tended to tunnel through a succession of floral tubes and bracts inward toward the center of the head where it passed the third instar feeding on a centrally located achene. When several larvae infested the same head, instead of feeding gregariously clustered in a single, central chamber like *T. conjuncta* (Goeden 1987), they remained separated but centralized while feeding.

The mature heads of *B. juncea* are small, i.e., 1–2 cm in dia. (Benson and Darrow 1981). Twenty-three capitula collected from Fossil Canyon, Imperial Co., on 11 i 1987 contained an average of 17 (range, 9 to 27) achenes. However, usually at least some achenes in a head, even one infested by several larvae, remained unattacked. Some receptacles were shallowly scarred by larval feeding, a phenomenon noted and currently being assessed quantitatively with *Paracantha gentilis* Hering in capitula of *Cirsium californicum* Gray (D. H. Headrick and R. D. Goeden, unpublished data). As with other *Trupanea* studied (Cavender and Goeden 1982, Goeden 1987), larvae of *imperfecta* usually oriented with their heads directed outward away from the receptacles after they stopped feeding before pupariating (Fig. 1b and 1c).

*Pupa.*—The puparium (Fig. 1c and 1d) is black, ellipsoidal, smoothly rounded at both ends, superficially smooth, but distinctly segmented, much like *T. conjuncta* (Goeden 1987). Thirty-one, field-collected puparia measured  $2.6 \pm 0.04$  (range, 2.1–3.3) mm in length by  $1.2 \pm 0.02$  (range, 0.9–1.3) mm in greatest width. Thus, the puparia of *T. imperfecta* are shorter and narrower than those of both *T. bisetosa* and *T. conjuncta* (Cavender and Goeden, 1982, Goeden 1987).

Puparia from which adults emerged remain attached for months to the dried, open heads that have shed their achenes (Fig. 1d), thus forming units readily sampled and counted to determine infestation rates. Accordingly, a total of 555 infested heads, collected from three locations, contained an average of 2 (range, 1 to 9) puparia. Most puparia were borne centrally, < 1 mm above and perpendicular to the receptacle surface, frequently with their posterior ends tightly appressed within the concave basal remains of one or two achenes (Fig. 1c). In heads that bore more than one puparium, these cases usually were glued together lengthwise and staggered (Fig. 1d), or were affixed to opposite sides of centrally located, receptacle bracts. Although most puparia were located centrally, a few were formed on the peripheries of multi-infested heads.



*Adult.*—Adults of *T. imperfecta* are readily recognized by their sexually dimorphic wing patterns. This pattern is considerably reduced in the male (Figs. 1e, 1f).

Males and females, newly emerged from mature heads, are sexually immature and apparently do not mate, much like *T. conjuncta* (Goeden 1987). From analysis of rearing records for 555 males and 509 females from 33 samples of capitula collected at Chino Canyon during 1983–84, the sex ratio appears to be slightly male biased, as reported for *T. conjuncta* (Goeden 1987), although statistically not significant [ $\hat{p} = 0.478\%$  ♀♀, SE ( $\hat{p}$ ) = 0.015, 95% c.l. = 0.508–0.448]. Males emerged along with females throughout their emergence periods, as determined from daily records of adults reared from the 33 samples, and as also reported for *T. conjuncta* by Goeden (1987).

Normally, flowering by *B. juncea* terminates and the plants go dormant in the low-elevation Colorado Desert in late spring (June). At this time, the newly emerged adults migrate to higher elevations, many following drying water courses upward into surrounding mountains. There, these long-lived adults pass the summer foraging along streams and in meadows, as they apparently remain in reproductive diapause. On three different years, both sexes were swept in low numbers from damp, grassy meadows at ca. 3000 m on San Gorgonio Mountain in mid-summer (July and August), at locations well removed from *B. juncea* inhabiting canyons and washes on the southern and eastern, basal slopes of this mountain.

During autumn, perhaps in response to shorter daylengths or lower temperatures in the mountains, the flies migrate downward and congregate on and near *B. juncea*, which by December and January already is responding to winter rainfall and resuming vegetative growth and flower bud production. Presumably mating occurs at this time, although this behavior was not observed in the field or in insectary cagings.

Oviposition was observed in the field on several occasions. The female usually initiated oviposition and obtained purchase on a young capitulum by placing the tip of her oviscape downward in the notch formed by two overlapping outer phyllaries. Repeated thrusts of the ovipositor brought its tip to one of the sites within the head previously described, where from one to three eggs were laid at a single insertion. Ovipositions by nine different females lasted an average of 45 (range, 28 to 93) sec. These females remained motionless with their wings held tightly overlapped, horizontal, and backward over their dorsa during oviposition. Oviposition was observed in the field during the warmest parts of winter days (between 10:00 and 14:00 in February and March, 1985 and 1986). After ovipositing, the females characteristically rubbed their oviscapes and partly exerted ovipositors with their hind tarsi. During this post-ovipositional grooming, one female repeatedly touched the tip of her ovipositor to the apex of the bud in which she had just oviposited. This behavior may have involved deposition of a short term oviposition deterrent, as recently observed with *P. gentilis* (Headrick and Goeden, unpublished data), and needs to be addressed experimentally.

*Seasonal history.*—As documented above by the sample dates for Chino Canyon, more than one generation may be produced per year. In 1983, flowering by *B. juncea* as well as reproduction by *T. imperfecta* continued locally all year on plants growing close to a continuously flowing stream. However, more typically, and as had occurred with plants growing above and away from the stream in 1983, reproduction by *T. imperfecta* and its host plants dwindled then ceased in June along with the waterflow following a winter with less rainfall in 1984. This demonstrated that reproduction by *T. imperfecta* is facultative and closely associated with and stimulated by the

presence of its flowering host plant. Facultative voltinism was reported for other stenophagous, desert-inhabiting Tephritidae, i.e., a gall-forming *Procecidochares* sp. (Silverman and Goeden 1980) and *T. conjuncta* (Goeden 1987).

*Mortality factors.*—As reported for *T. conjuncta* (Goeden 1987), jumping spiders (Araneida: Salticidae) and crab spiders (Araneida: Thomisidae) appeared to be the most common predators of adults observed on the preblossom and flowering host plants. Several species of parasitic Hymenoptera were reared from capitula of *B. juncea* infested by *T. imperfecta*. Species positively identified as parasites of *T. imperfecta* include: *Horismenus* sp. (Eulophidae), a solitary, hyperparasite; *Eurytoma* sp. and *E. vernonia* Bugbee (Eurytomidae), solitary, primary, larval or larval-pupal endoparasites; *Pteromalus* (*Habrocytus*) *purpureiventris* (Ashmead) (Pteromalidae), a solitary, primary, larval ectoparasite; *Mesopolobus* sp. (Pteromalidae), a solitary, facultative primary/hyperparasite; and *Torymus* sp. (Torymidae), a rare, solitary, larval ectoparasite. *Eurytoma* sp., *E. vernonia*, and *P. purpureiventris* also parasitized *T. conjuncta* in heads of *Trixis californica* (Adams) at desert locations where both plant species were found (Goeden 1987).

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